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BODY FORM AND GAIT IN TERRESTRIAL VERTEBRATES¹

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One appeal of pure research is that in answering certain questions, new problems arise, and one is led on and on into a progressively deeper study of a problem. Certain aspects of terrestrial locomotion can be viewed as an example of how research in this area has shifted from description to quantitative analysis and on to a consideration of the interrelationships between form and function. Much research in anatomy today is at the functional level, that is, it is a search for an explanation of structure in terms of the functions the structures are performing, and the intermeshing of certain structures and their functions with those of other parts of the organism.

My research animal has been the Central Painted Turtle (*Chrysemys picta marginata*). In common with other terrestrial ectotherms, turtles carry their body close to the ground when they walk, but turtles are unique in being encased in a protective shell. Corollaries of the shell are a short, broad, and rigid trunk, and these features have important locomotor consequences.

Locomotion was studied first not in turtles but in mammals. Careful analyses of locomotion can be traced back to Eadweard Muybridge's study of horse gaits, which he began in 1872 (Muybridge, 1887). Muybridge was a photographer who, in a period preceding ciné photography, devised an ingenious battery of 24 still cameras that could be triggered in quick succession to produce a series of still pictures indicating the sequence of limb movements (fig. 1). Muybridge was sponsored by Leland Stanford (after whom Stanford University was named), for Stanford, a breeder of race horses, was interested in the question of whether or not a moving horse had all four feet off of the ground at any time in any of its gaits.

Notable among Muybridge's successors was Howell, who in 1944 made a careful analysis of gaits in terms of foot fall or support patterns. To understand this analysis, the pattern during one stride of a common type of walk used by a four-footed mammal must be considered. A stride represents the period from the placement of one foot upon the ground to the next such placement of the same foot. A walking stride is divided into eight stages representing different numbers and combinations of feet upon the ground (fig. 2A). It is conventional to start a stride analysis with the placement of the left hind foot. The animal is then supported by three feet. The right hind foot is next removed, leaving two supporting feet. The placement of the left front foot again provides three supporting feet, but the combination of feet is different from that in the first stage. The sequence of foot placement during the full stride are left hind, left front, right hind, right front. There is an alternation between three- and two-footed support

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stages, and the two-footed stages are of two types: diagonally opposite feet (eg., left hind and right front), and ipsilateral feet (eg., left hind and left front).

In a perfect trot (fig. 2B), which is a much more rapid gait than a walk, the diagonally opposite two-footed stages alternate with stages in which no feet are on the ground (Howell, 1944). The three-footed stages are omitted. In a pace, another fast gait (fig. 2C), ipsilateral two-footed stages alternate with unsupported stages.

Support patterns are purely descriptive of which feet are on and off the ground. Hildebrand (1962, 1965) has shown that the duration of foot placement and withdrawal are also variable. Support patterns together with the time factor can be represented in a gait diagram (fig. 3). In a gait diagram of a turtle walking (Walker, 1971), it can be seen that the foot-fall sequence is the same as in a horse (left hind, left front, right hind, right front), but there are four-footed stages that replace the ipsilateral two-footed stages of the horse. Duration of foot contact is also shown, and it is quite long. Each foot is on the ground for six stages and

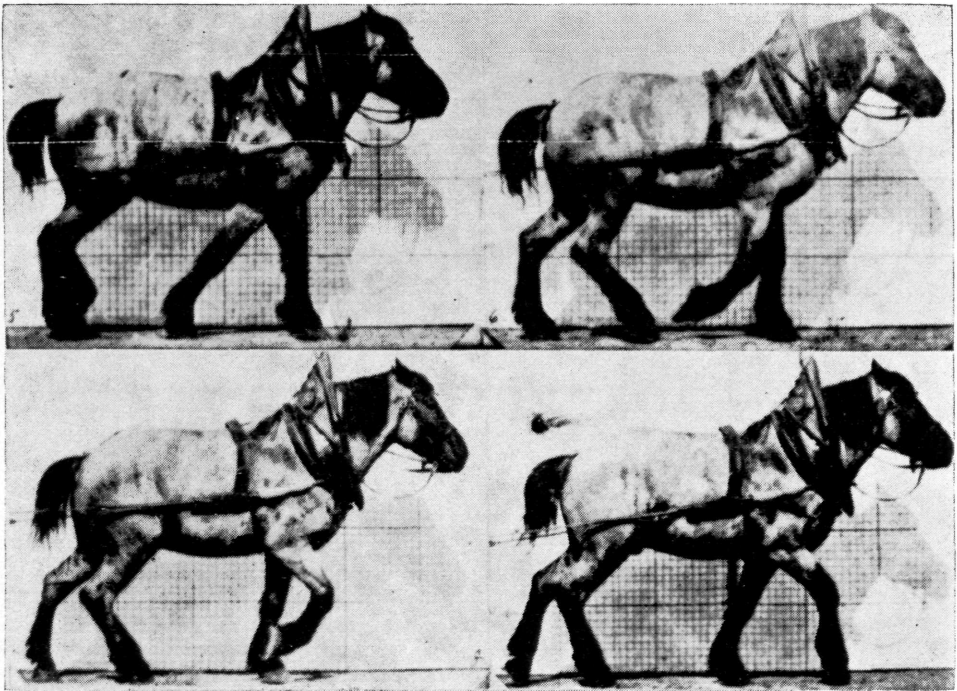


FIGURE 1. Four successive photographs of the limb movements of a walking horse pulling a load (from Muybridge, 1887, courtesy Dover Publications, New York).

off for only two. We have seen that the fastest gaits (the trot and pace) are those with the least foot contact with the ground. A comparable fluctuation in velocity is evident within a stride. Deceleration occurs in stages 8 to 1 and 4 to 5 when there is a shift from three to four feet on the ground; acceleration occurs in stages 2 to 3 and 6 to 7 when there is a shift from three to two feet. Alternating periods of acceleration and deceleration suggests that this type of gait may be more expensive in energy consumption than are ones with fewer combinations of feet upon the ground, and probably less sharp changes in velocity; however, data are not yet available on velocity changes within trots and paces, or on comparative energy expenditures.

Analysis of locomotion has been made more quantitative by Hildebrand (1965), who showed that all the information in a gait diagram can be expressed in two numbers representing a gait formula. The first variable is the percent of the total stride interval that the left hind foot is on the ground. Other feet would be on the ground for approximately the same interval if the gait were symmetrical, as

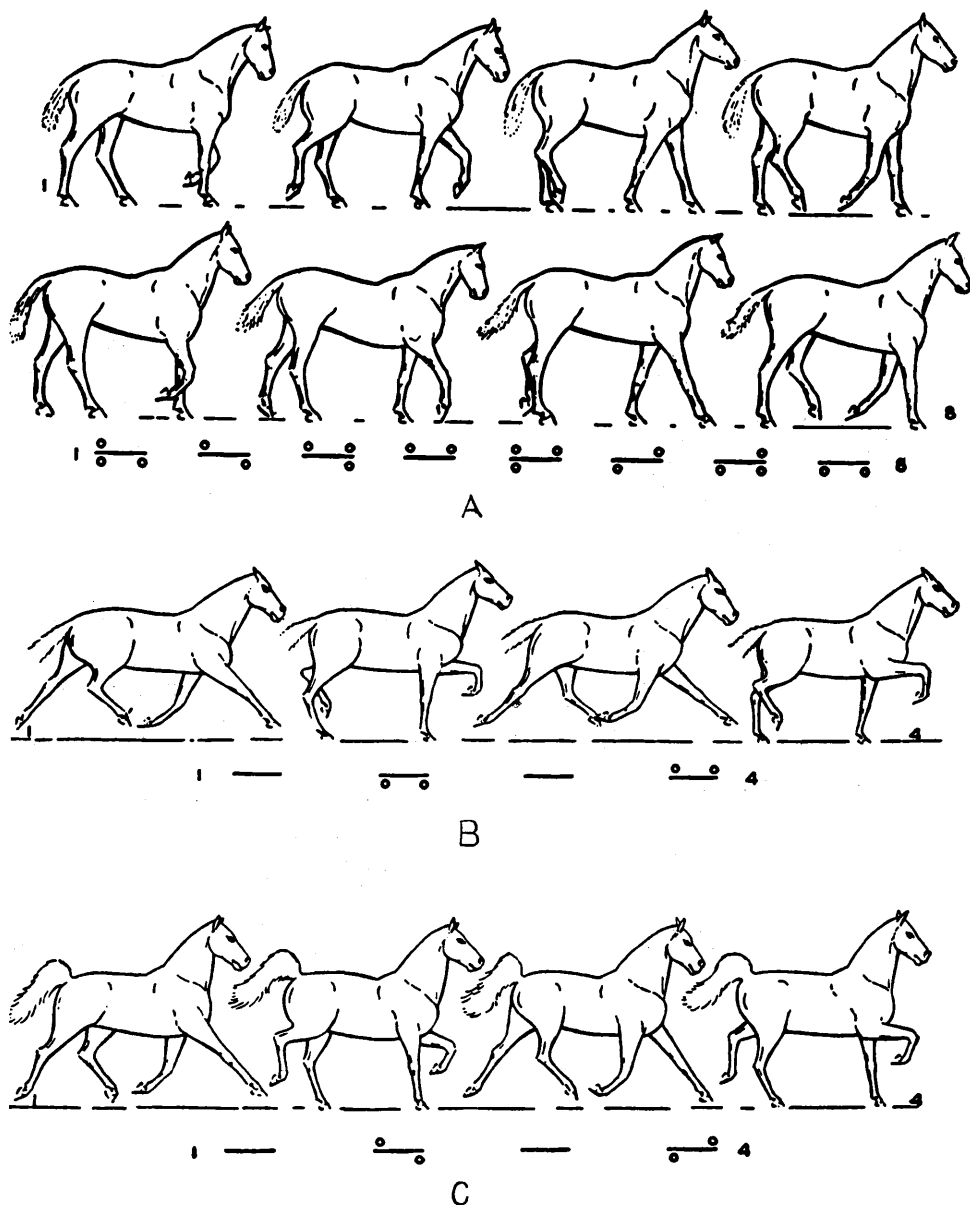


FIGURE 2. Three common, symmetrical gaits of a horse: A, a moderately fast walk; B, a running trot; C, a running pace. The gaits are shown in lateral views and by diagrams of the support-pattern sequences, that is, the combination of feet upon the ground (from Howell, 1944, courtesy University of Chicago Press, Chicago).

are the gaits under consideration. For the turtle stride studied in Figure 3, foot contact is about 80 percent of the stride. This figure is a measure of the average speed the animal is travelling. As it decreases, the animal moves faster. The second value in the gait formula indicates the percent of the total stride interval that the placement of the front foot follows that of the hind foot on the same side of the body. In the turtle gait illustrated, it is 38 percent of the stride. If this interval is long (30 to 45 percent of the stride), the placement of the right hind foot, which occurs near the middle of the stride, follows very soon after the placement of the left front foot. As a consequence, diagonally opposite legs are doing very nearly the same thing; they are, to quote Hildebrand, "related in time as a pair."

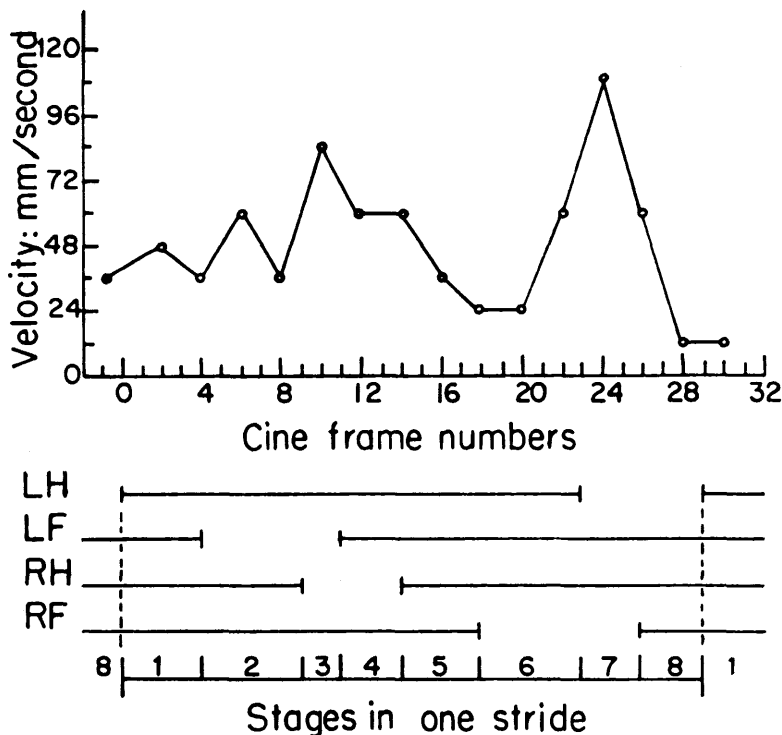


FIGURE 3. Analysis of a stride in the turtle taken from ciné films exposed at 24 frames per second. The lower part of the figure is a gait diagram showing by lines the portion of a stride during which each foot is on the ground. Abbreviations: LH, left hind foot; LF, left front; RH, right hind; RF, right front. Changes in velocity during the eight stride stages are shown in the upper half of the figure. Lower and upper diagrams are coordinated in time. (From Walker, 1971.)

Hildebrand has graphed nearly 1000 gait formulas of mammals and a few reptiles and amphibians. Gait formulas are not uniformly distributed in the area of the graph, but cluster in a distinct pattern indicated by the clear area in Figure 4. Foot contact, which is a measure of speed, ranges from about 90 to 20 percent of the stride interval. If it is too long, the animal is barely moving; if too short, the animal would have little support. The fastest symmetrical gaits are the running pace and the running trot, in which duration of foot contact can fall as low as 20% of the stride interval, and the number of feet on the ground can alternate between two and zero.

The lag in the placement of the front foot on the same side of the body is a measure of the support sequence, or gait. When it is close to zero, the front foot is being placed on the ground at the same time as the hind foot, i.e., the animal is pacing. As this interval increases, the front foot follows the hind foot on the same side of the body, and the gaits are said to be in lateral sequence. At first the front foot is moving most of the time with the ipsilateral hind foot in a lateral

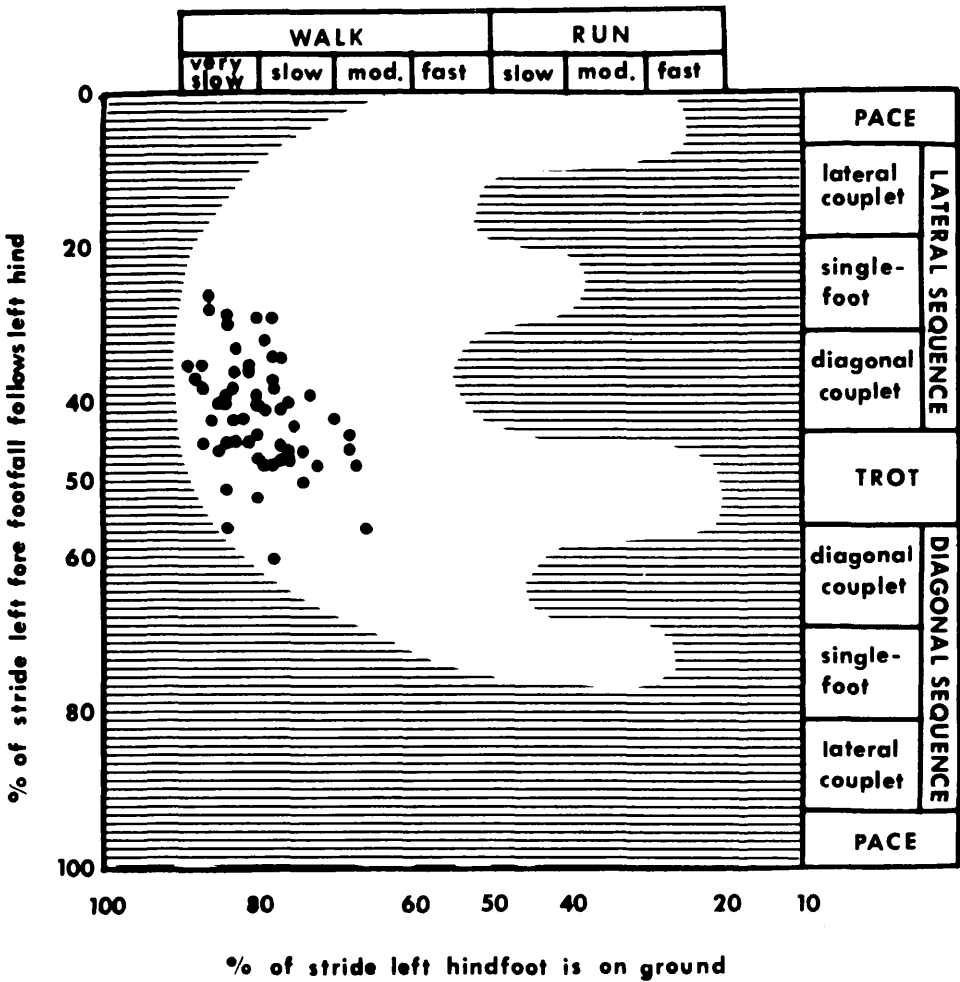


FIGURE 4. A graph of the distribution of gait formulas. Hildebrand (1965) has found that 162 formulas for horses and 833 for other animals belonging to 158 genera fall within the clear area. Zug's findings on the distribution of formulas for 19 species of cryptodire turtles are indicated by black dots (from Zug, 1971).

couplet gait. As the interval increases more, the front foot gets out of phase with the ipsilateral hind foot, producing a single-footed gait. As the interval increases still more, the front foot begins to move with the contralateral hind foot in a diagonal couplet gait. As the interval approaches 50 percent, the front foot and contralateral hind foot move in synchrony and the animal is trotting.

The gaits of 19 species of cryptodire turtles have been studied by Zug (1971);

when plotted, they cluster in the area shown by black dots in figure 4. No turtle can pace, though many can trot, but the favored gait is a lateral-sequence, diagonal-couplet, slow walk. Here a correlation between form and function is evident. This type of walk maximizes stability, a condition that is important to a turtle whose broad trunk is carried close to the ground.

This stability principle was discussed by Gray in 1944, and was described as the triangle of support. According to this concept, maximum stability is achieved when there is a tripod of three feet upon the ground, with the center of gravity lying within that tripod (fig. 5). The turtle, during four of the eight stride stages,

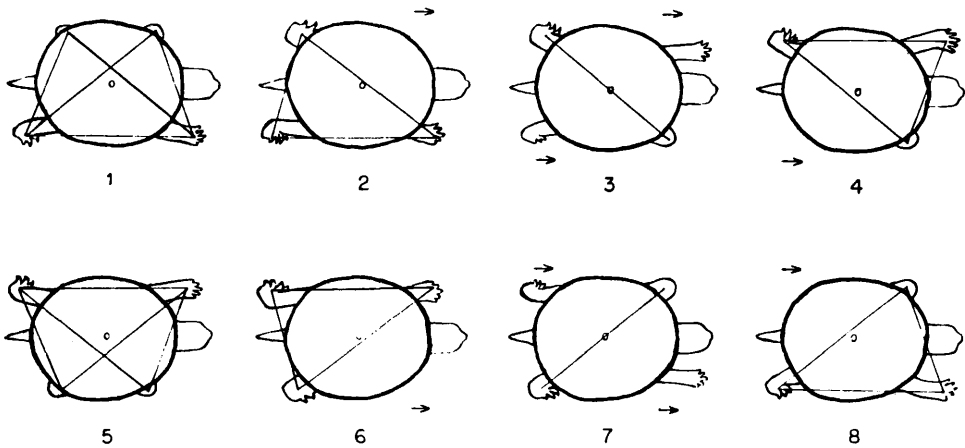


FIGURE 5. Dorsal views of the sequence of support patterns during one stride of a lateral-sequence, diagonal-couplet walk of *Chrysemys picta marginata*. The animal's center of gravity is indicated by a small, open circle; lines connect feet upon the ground; and arrows indicate the movement of feet off of the ground (from Walker, 1971).

is supported by triangles of this type (Walker, 1971). The two-footed stages represent transitions from triangles of support based on one side of the body to triangles of support based on the opposite side. There is a moment of instability during the transition from one of these to the other, but the turtle is moving at maximum velocity at this time (fig. 3), and its center of gravity is crossing the diagonal between the two supporting feet. The two four-footed stages represent transitions between triangles based on the same side of the body. The turtle is placing a hind foot to establish a new triangle before removing a front foot and abandoning the existing triangle. The alternative would be to try and remain balanced on two ipsilateral feet. As was demonstrated earlier (fig. 1A), this option is utilized by a mammal whose trunk is carried well above the ground; a slight toppling to one side in such a case would be of little consequence. On the other hand, this would be a difficult option for a typical amphibian or reptile moving close to the ground, and it probably would not be possible for a turtle with such a broad trunk. The center of gravity would be so far from the two ipsilateral supporting feet that one side would surely drag heavily upon the ground. Since a pace is an alternation of ipsilateral two-footed stages, a turtle cannot pace.

The contralateral two-footed stages provide a bit more stability, for the center of gravity is on or close to a diagonal between two supporting feet. As the turtle lunges forward, it is prevented from nosing into the ground by a quick placement of a front foot. Alternation of these stages constitute a trot, and some turtles can trot. The favored gait, however, is the lateral-sequence, diagonal-couplet walk, which maximizes stability, but does so at the expense of speed of travel.

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